Odonatologica 20(4): 441-452 *December 1, 1991*

EGG CHORIONIC STRUCTURES IN CORDULIIDAE AND LIBELLULIDAE (ANISOPTERA)

J.W.H. TRUEMAN
Department of Zoology, Australian National University,
P.O. Box 4, Canberra, A.C.T. 2601, Australia

Received March 22, 1991 / Accepted May 9, 1991

Eggs of 11 Australasian Corduliidae and 7 Libellulidae, referable to 8 subfamilies, are described or redescribed, using light and scanning electron microscopy. Inconsistencies in existing libelluloid eggshell nomenclature are noted and a revised nomenclatural scheme is proposed.

INTRODUCTION

Eggs from small numbers of libelluloid species have previously been described using light microscopy (e.g. TILLYARD, 1917; ANDO, 1962; CORBET, 1962; HINTON, 1981) and several have recently been examined using scanning electron microscopy (SEM) (e.g. MILLER & MILLER, 1985; MILLER, 1987; IVEY et al., 1988) but the majority remain undescribed. The present paper utilises light microscopy and SEM to provide egg descriptions for eighteen Australasian species representing four corduliid subfamilies (Corduliinae, Cordulephyinae, Gomphomacromiinae and Synthemistinae) and four libellulid subfamilies (Brachydiplacinae, Libellulinae, Sympetrinae and Tetrathemistinae). Original descriptions are given for eggs of *Diplacodes haematodes* (Burm.), *D. melanopsis* (Martin), *Eusynthemis brevistyla* (Sel.), *Hesperocordulia berthoudi* Till., *Nannodiplax rubra* Br., *Nannophlebia risi* Till., *Nannophya dalei* Till., *Orthetrum caledonicum* (Br.), *Pentathemis membranulata* Karsch, *Procordulia jacksoniensis* (Ramb.), *Synthemis eustalacta* (Burm.) and *S. regina* Sel. Redescriptions or extensions to descriptions are given for eggs of *Diplacodes bipunctata* (Br.), *Hemicordulia australiae* (Ramb.), *H. tau* (Sel.), *Procordulia grayi* (Sel.) and *P. smithii* (White). The previous description (TILLYARD, 1911; CORBET, 1962) for eggs of *Cordulephya pygmaea* Sel. is substantially revised. Descriptions include notes on development where available.

Comparison of present observations against previous egg descriptions indicates that although the composition of the libelluloid egg varies little from species tot species or across wider groupings, confusion exists regarding the naming of egg structures and opinions differ as to where the boundary between the egg and surrounding material of extrachorionic origin should be drawn. These issues are reviewed and a corrected general nomenclatural scheme for the libelluloid egg is proposed.

METHODS

Eggs of *C. pygmaea, D. bipunctata, D. haematodes, D. melanopsis, E. brevistyla, H. australiae, H. tau, N. risi, N. dalei, O. caledonicum, P. jacksoniensis, S. eustalacta* and *S. regina* were obtained from captured females by repeatedly dipping the abdomen into water. Totals of between 500 and 2000 eggs were obtained from between 1 and 6 females of each species. Some eggs were collected and immediately preserved by dipping the abdomen into 70% ethanol after starting a flow of eggs by dipping in water. Water-collected eggs were incubated in tap, pond or river water and daily samples preserved in 70% ethanol. Subsamples of the eggs of 2 species (*D. melanopsis, H. australiae*) were manipulated by removal of the outermost chorionic layers during incubation, removal being effected by rolling each egg against a drop of glue, splitting the outer chorion with a pin, and expressing the inner parts intact. The above adults and eggs are in the author's collection.

Eggs of *N. rubra* (N = 52) were located externally on terminal segments of a female preserved in 70% ethanol in the author's collection. Eggs of *P. grayi* (N = c. 200) and *P. smithii* (N = c. 300) were obtained in 75% ethanol from the collection of the Auckland Institute and Museum. Eggs (N = 15) of *H. berthoudi* were obtained by dissection of a dried specimen and eggs (N = 28) of *P. membranulata* were found attached to terminal segments of a dried specimen in the Australian National Insect Collection.

Live eggs were mounted in water on cavity slides for light microscopy. Preserved eggs were examined on cavity slides, whole or fragmented, in either water, 70% ethanol or 50% glycerol, and fragments mounted on conventional slides in 50% glycerol. Some eggs were treated with 10% potassium hydroxide to remove gelatinous layers and inter-egg gelatinous stands before mounting.

Most eggs and egg fragments for SEM were taken through graded ethanols to 100% ethanol, air dried, mounted with nail varnish on aluminium stubs, and gold coated for observation in a Cambridge 360 scanning electron microscope. To avoid partial collapse of the thin outer layers a few whole, preserved eggs were rehydrated over 2-3 days, wetmounted on aluminium stubs, snap-frozen in nitrogen slush and placed in the vacuum chamber of the Cambridge 360 SEM cooled with liquid nitrogen. The temperature was raised to -80°C for 3-4 minutes in vacuo to remove ice crystals, and the specimens then sputter coated with gold. Electron micrographs were taken with specimens at temperatures about -98°C.

Whole egg measurements were taken on both live and preserved eggs using an Olympus BH2 compound microscope with ocular micrometer. Further whole egg, micropylar and chorion thickness measurements were taken using SEM software or from scanning electron micrographs.

EGG STRUCTURE

As appears from the literature and observations summarised in the next section, and as shown in Figure 1, the generalised libelluloid egg is more or less ellipsoidal, with an anterior, hollow, conical projection (micropylar projection)

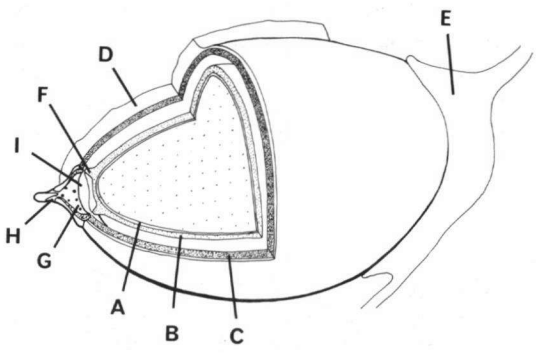


Fig. 1. Cutaway view of the generalised libelluloid egg: (A) vitelline membrane, — (B) endochorion, — (C) exochorion, — (D) exochorionic jelly (some species), — (E) strand jelly (some species), — (F) pedicel, — (G) micropylar projection, — (H) atrial opening, — (I) micropylar atrium.

but without surface ornamentation. The eggshell comprises two thin membranes (endochorion, exochorion) which may or may not be in contact but are never conjoined. A gelatinous matrix may be present on the exochorion or as connecting strands between eggs. Two openings (atrial openings) on the micropylar projection are presumed sites of sperm entry to a space (micropylar atrium) formed between the underside of the projection and a ring-shaped ridge (pedicel) on the underlying endochorion. Shallow depressions on the endochorionic surface within the pedicel are tentatively identified as micropyles.

EGG DESCRIPTIONS

Cordulephya pygmaea (Figs 2-4): Previous figure a handlens image, (TILLYARD, 1911) redrawn in CORBET (1962); erroneously interpreted by Tillyard as showing a sculptured surface and by Corbet as showing irregular chorionic dimpling and a broad, basal attachment disc.

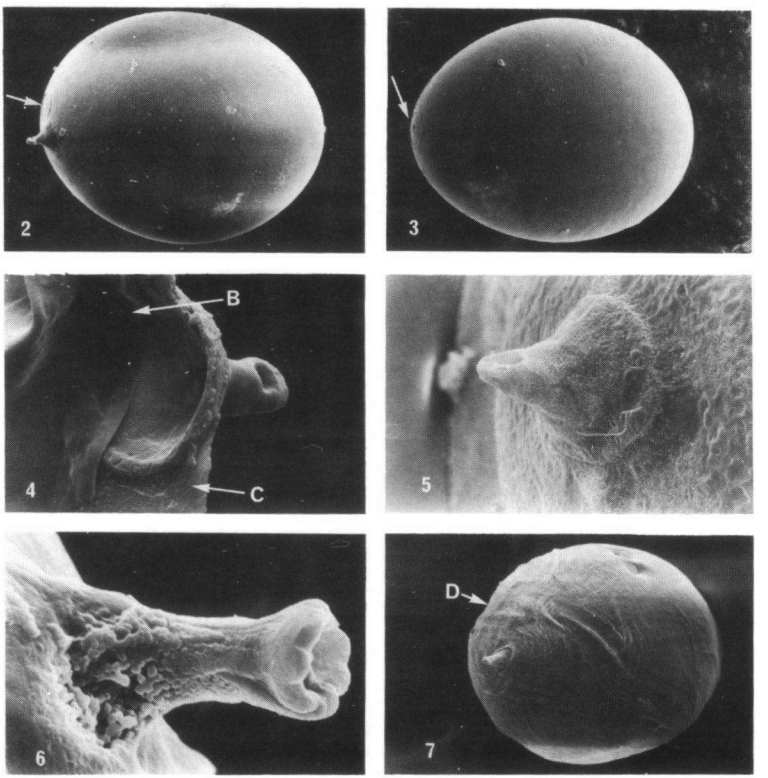
Egg sub-spherical, length/width ratio 1.25:1 or less, declining slightly during development. Endochorion smooth, flattened anteriorly within ring formed by pedicel, pale yellow turning orange-brown and gradually darkening; dimensions 0.39x0.31 to 0.40x0.34 mm at 4 days. Pedicel prominent. Exochorion very thin, smooth, transparent; apposed to endochorion throughout development. Micropylar projection 18 μm high, a concave-sided cone with bulbous tip. Atrial openings two, opposite, subapical. Exochorionic gelatinous layer very thin; the eggs are sufficiently sticky to accumulate fine debris which is not then readily removable. Strand jelly absent. Eclosion in 17-20 days at 24°C, a few to 31 days.

Diplacodes bipunctata: Previous figure: TILLYARD, (1917: 228); short description and figure, ROWE (1987: 195).

Egg ellipsoidal becoming sub-spherical; length/width ratio declining from 1.6:1 to 1.2:1 during development. Endochorion smooth, colourless to pale yellow, turning orange-brown and gradually darkening; dimensions 0.38x0.30 to 0.40x0.32 mm at 4 days. Pedicel not prominent. Exochorion very thin, smooth, transparent; apposed to endochorion throughout development yet allowing inner

and outer layers to become misaligned on occasion. Micropylar projection a concave-sided cone, 24 μm high. Atrial openings two, opposite, apical. Gelatinous layer very thin. Eggs only slightly sticky. Strand jelly absent. Eclosion in 18-20 days at laboratory temperatures.

D. haematodes (Fig. 5): No previous description.
Egg indistinguishable from *D. bipunctata.* Eclosion in 12-18 days at 24°C.



Figs 2-7. Eggs of some Libelluloidea: (2) *Cordulephya pygmaea,* whole egg imaged using cold-stage SEM: endochorion and exochorion have become misaligned, the pedicel causes a raised ring (arrowed) to show in the thin exochorionic surface; — (3) same, endochorion imaged using cold-stage SEM: pedicel arrowed; — (4) same, inner surface of micropylar projection: (C) exochorion, (B) endochorion; — (5) *Diplacodes haematodes,* micropylar projection: overall shape and placement of atrial openings varies little across species examined, except in the Synthemistinae; — (6) *Eusynthemis brevistyla,* micropylar projection: this shape is common to all Synthemistinae examined; — (7) *Hemicordulia australiae,* whole egg: the outer coating (D) is of exochorionic jelly expanded in water before being prepared for SEM by the method described in the text.

D. melanopsis: No previous description.

Egg similar to *D. bipunctata,* but in later stages surrounded by exochorionic jelly to 0.05 mm thick covering whole egg except tip of micropylar projection. Eclosion in 27-43 days at laboratory temperatures. Mechanical removal of the exochorion 6-10 days after oviposition (21-36 days prior to hatching) has no noticeable effect on hatching success.

Eusynthemis brevistyla (Fig. 6): No previous description.

Egg sub-spherical, length/width ratio 1.25:1 to 1.2:1, anteriorly somewhat flattened when newly laid. Endochorion smooth, grey, turning pale pink after about 6 hours and yellow-brown after 2-3 days; dimensions 0.51x0.42 to 0.52x0.43 mm at 4 days. Pedicel not prominent. Exochorion very thin, smooth, transparent, non-expanding; apposed to endochorion throughout development yet allowing inner and outer layers to become misaligned on occasion. Micropylar projection hyperboloid, 20-22 μm high. Atrial openings two, adjacent, recessed, located on the apical surface of the micropylar projection. Gelatinous layer very thin, non-expanding. Eggs only slightly sticky. Strand jelly absent. Eclosion in 19-20 days at laboratory temperatures.

Hemicordulia australiae (Fig. 7): Previous descriptions and figures: ARMSTRONG (1958); ROWE (1987: 185).

Egg ellipsoidal with anterior and posterior protuberances when laid, sub-spherical at hatching; length/width ratio declining from 2.0:1 to 1.1:1 during development. Endochorion smooth, grey, turning light brown after 1 day; dimensions 0.46x0.30 to 0.52x0.33 mm at 4 days. Pedicel prominent, hyaline, with a somewhat elevated floor. Exochorion thin, smooth, transparent, non-expanding; separated 0.03-0.04 mm from endochorion except at poles. Micropylar projection a concave-sided cone, 25-27 μm high. Atrial openings two, approximately 120° apart, sub-apical. Eggs connected posteriorly by thin, fine jelly which can be drawn out in strands to 3-5 cm. Exochorionic jelly becoming sticky after 1-4 hours in water, expanding slowly to approximately 0.2 mm thick after 4-5 days (at 24°C). Egg clumping occurs when exochorionic jelly layers of adjacent eggs coalesce or strand jelly becomes tangled. Eclosion in 11-15 days at 24°C, a few eggs in centre of egg clumps taking to 30 days; eclosion in 19-21 days at laboratory temperatures. Mechanical removal of the exochorion 6-10 days after oviposition (6-10 days prior to hatching) has no noticeable effect on hatching success.

H. tau: Previous figure: a small-scale drawing showing egg outline with jelly either removed or not expanded (TILLYARD, 1917: 228).

Similar to eggs of *H. australiae* and following a similar developmental pattern. Distinguishing features: (i) egg slightly smaller, endochorion 0.45x0.30 to

0.49x0.32 mm at 4 days, (ii) atrial openings more or less opposite and closer to apex of micropylar projection, (iii) strand jelly stronger and more sticky; the eggs more liable to clump together. Eclosion in 9-21 days at 24°C, 17-19 days at laboratory temperatures.

Hesperocordulia berthoudi: No previous description.

Egg ellipsoidal. Endochorion dark brown in dried specimens, dimensions 0.45x0.30 mm. Exochorion fairly thin, smooth, transparent, dimensions 0.45x0.35 mm in rehydrated specimens. Micropylar projection a concave-sided cone, 55 μm high. Atrial openings two, opposite, sub-apical. Gelatinous layer not observed.

Nannodiplax rubra: No previous description.

Egg ellipsoidal. Endochorion light brown in preserved specimens, dimensions 0.40x0.30 mm. Exochorion thin, smooth, transparent. Micropylar projection a concave-sided cone, 28-30 μm high. Atrial openings two, opposite, sub-apical. Gelatinous layer not observed.

Nannophlebia risi (Fig. 8): No previous description.

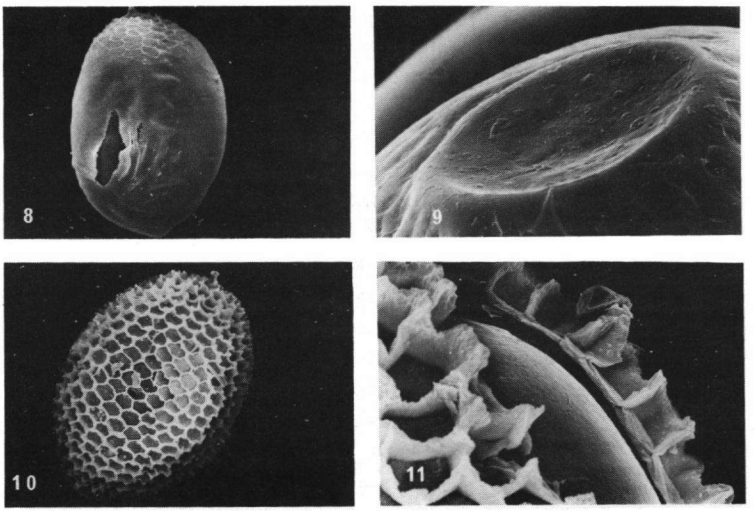
Egg sub-spherical, length/width ratio 1.2:1 not changing significantly during development. Endochorion smooth, pale yellow, turning orange-brown; dimensions 0.34x0.28 to 0.36x0.28 mm at 4 days. Pedicel not prominent. Exochorion very thin, smooth, with faint outlines of follicle cell impressions around anterior pole, transparent; apposed to endochorion throughout development. Micropylar projection a concave-sided cone 15 μm high. Atrial openings two, opposite, close to tip of micropylar projection. Outermost layer not gelatinous, the eggs non-sticky. Strand jelly absent. Eclosion in 16-31 days at 24°C.

Nannophya dalei: No previous description.

Egg ellipsoidal, length/width ratio declining from 2.1:1 to 1.8:1 during development. Endochorion smooth, pale yellow, turning orange brown; dimensions 0.60x030 to 0.62x0.31 mm at 4 days. Pedicel not prominent. Exochorion thin, smooth, transparent; apposed to endochorion throughout development. Micropylar projection a concave-sided cone, 35-36 μm high. Atrial openings two, opposite, subapical. Gelatinous layer thin: the eggs will stick to a pin and readily accumulate fine debris. Strand jelly absent. Eclosion in 24-26 days at laboratory temperatures.

Orthetrum caledonicum: No previous description.

Egg deformable when laid, becoming ellipsoidal with length/width ratio 1.8:1 after 1-2 days, declining to 1.3:1 at hatching. Endochorion smooth, grey to pale yellow, turning dark brown over 4-5 days; dimensions 0.45x0.30 to 0.45x0.35 mm



Figs 8-11. Eggs of some Libelluloidea: (8) *Nannophlebia risi,* whole egg: follicle cell impressions are visible around the anterior pole, and the exochorion has been torn to reveal part of the endochorionic surface; — (9) *Procordulia smithii,* pedicel region of endochorion; — (10) *Synthemis regina,* whole egg; — (11) same, sectioned view of exochorion.

at 4 days. Pedicel not prominent. Exochorion very thin, smooth, transparent, non-expanding; separated 0.01-0.02 mm from endochorion when laid, but the endochorion expands to fill this gap after 1-2 days. Micropylar projection a concave-sided cone 27 μm high. Atrial openings two, opposite, almost conjoined, apical. Outermost layer not gelatinous, the eggs non-sticky. Strand jelly absent. Eclosion in 13-20 days at 24°C, a few to 41 days.

Pentathemis membranulata: No previous description.

Egg ellipsoidal. Endochorion dark brown in dried specimens, dimensions 0.40x025 mm. Pedicel not prominent. Exochorion thin, smooth, transparent. Micropylar projection a concave-sided cone, 25-26 μm high. Atrial openings two, opposite, sub-apical. Gelatinous layer not observed.

Procordulia grayi: Previous descriptions and figures: ARMSTRONG (1958); ROWE (1987: 164). Egg strand structure described, WINSTANLEY (1981).

Egg pear-shaped, narrowed anteriorly. Endochorion 0.69x0.49 to 0.86x0.58 mm; preserved specimens dark brown. Pedicel not prominent. Exochorion fairly thin, smooth, transparent, widely separated from endochorion in preserved specimens; exochorion 0.98x0.63 to 1.11x0.79 mm in preserved specimens. Eggs often with long axis of endochorion at an angle to that of exochorion. Micropylar projection a concave-sided cone, 60 μm high, lightly tanned in preserved speci-

mens. Atrial openings two, opposite, sub-apical. Eggs connected in a strong, resilient gelatinous matrix approximately 0.4 mm thick.

Procordulia jacksoniensis: No previous description.

Egg ellipsoidal becoming sub-spherical, length/width ratio declining from 1.7:1 to 1.2:1 during development. Endochorion smooth, grey, turning brown and gradually darkening; dimensions 0.43x0.31 to 0.48x0.36 mm at 4 days. Pedicel not prominent. Exochorion thin, smooth, transparent, loose around anterior pole, elsewhere remaining apposed to endochorion. Micropylar projection a concave-sided cone, 25 μm high, thickened around atrial openings. Atrial openings two, almost opposite, sub-apical. Exochorionic jelly not apparent at oviposition, but eggs slightly sticky after 1 day; a sticky gelatinous layer to 0.2 mm thick develops by day 3 enclosing whole egg including micropylar projection. Strand jelly absent. Eclosion in 13-18 days at 24°C.

P. smithii (Fig. 9): Previous descriptions and figures: ARMSTRONG (1958); ROWE (1987: 173-174).

Egg ellipsoidal. Endochorion dark brown in preserved specimens; dimensions 0.59-0.45 to 0.62x0.45 mm. Pedicel not prominent. Exochorion fairly thin, smooth, transparent; separated from endochorion 0.06-0.08 mm in preserved specimens. Micropylar projection a concave-sided cone, 25 μm high. Atrial openings two, 120° apart, sub-apical. Gelatinous layer strong, approximately 0.2 mm thick; tending thicker posteriorly.

Synthemis eustalacta: No previous description.

Egg ellipsoidal becoming sub-spherical, length/width ratio declining from 1.5:1 to 1.2:1 or less during development. Endochorion smooth, light grey, turning pink after 1 day and yellow-brown after 2-3 days; dimensions 0.54x0.47 to 0.56-0.49 mm at 4 days. Pedicel not prominent. Exochorion thin, smooth, transparent, loosely surrounding egg; separated by up to 0.05 mm from endochorion in later stages. Micropylar projection hyperboloid, 20 μm high. Atrial openings two, adjacent, recessed, located on the apical surface of the micropylar projection. Gelatinous layer tenuous, non-sticky, surrounding late-stage eggs to height of micropylar projection.

S. regina (Figs 10-11): No previous description.

Egg ellipsoidal, inner egg length/width ratio 1.6:1 when laid, declining to 1.4:1 at hatching. Endochorion smooth, grey, turning yellow-brown after 1-2 days; dimensions 0.60x0.32 to 0.64x0.32 mm at 4 days. Pedicel not prominent. Exochorion 3-5 μm thick, resilient, grey, non-expanding; dimensions 0.62x0.38 to 0.65x0.38 mm. Surface of exochorion covered in a conspicuous pattern of follicle cell impressions each about 20 μm across, separated by ridges 15-25 μm high.

Exochorion in contact with endochorion at poles but not equatorially. Micropylar projection hyperboloid, 23 μm high. Atrial openings two, adjacent, recessed, located on the apical surface of the micropylar projection. Gelatinous layer very thin, non-expanding, only slightly sticky; may be restricted to ridges between exochorionic surface cells.

EGG NOMENCLATURE

Insect eggs contain an oocyte plus various cell products, and are bounded by a chorion secreted from ovarian follicle cells. In some insect orders the egg receives additional spumaline coatings from gland cells in the oviduct during oviposition, but in Odonata, as is readily verified by dissection, all structures including the micropylar projection and external gelatinous layer are formed in the ovaries. The origin of inter-egg strand jelly is not known with certainty but as spumaline glands have yet to be found in the order (HINTON, 1981) this jelly may also be secreted by ovarian follicle cells.

The innermost part of the endochorion comprises a vitelline membrane, which becomes the fertilization membrane following entry of sperm. This membrane is seen in transverse SEM sections as a dense layer, without sub-structure, on the inner surface of the endochorion. The remainder of the endochorion is partly fibrous. The exochorion, which in some species is closely apposed to the endochorion but in others is only in contact at the poles, is also partly fibrous, and its outer surface carries follicle cell patterning in some species. The gelatinous layer (where present) arises from the egg surface by uptake of water and is structurally contiguous with the exochorion. The pedicel is an integral part of endochorion, but the micropylar projection, though attached to the exochorion, is separable by treatment with 10% KOH.

Previous authors have generally recognised all major structures, but inconsistencies in use of names and confusion over identification of outer structures as part of the egg are readily apparent. TILLYARD (1917) referred to structure A in Figure 1 as Vitelline Membrane, B+C as Chorion, D as Gelatinous Matter and F+G as Pedicel. ANDO (1962) called A Periplasm or Cortical Layer, B Vitelline Membrane, C Chorion, D+E Gelatinous and Adhesive Layer, and F+G Nipple-shaped Pedicel. BEAMS & KESSEL (1969) followed Ando's usage for B but divided the chorion into an Inner Dense Layer and an Outer Fibrous Layer. KAWASAKI et al. (1974) called B the Vitelline Membrane, C the Inner Chorion and D the Outer Chorion. HINTON (1981), apparently misinterpeting Beams and Kessel as to identity and ordering of layers, referred to B as the Inner Fibrous Layer of the chorion and C as the Outer Dense Layer, and regarded D+E as Spumaline. McCRAE & CORBET (1982) named B Chorion, C+D Spumaline, and G Spumaline Pedicel. WARINGER (1983) called G the Cone. WINSTANLEY (1981), following ARMSTRONG (1958), named C+D Gelatinous Mem-

brane and E the Gelatinous Core of the Egg Strand, while GONZALEZ SORIANO (1987) used Central Filament for the same structure. MILLER & MILLER (1985) identified B with Endochorion, C with Exochorion, and D with Spumaline, but MILLER (1987) considered B Vitelline Membrane, C Endochorion, and D Exochorion. Most recently, IVEY et al. (1988) provided a "general" description of the libelluloid egg based on the innermost layers only, treating all structures external to B as extrachorionic. In their nomenclature the outermost part of B becomes Exochorion, F Apical Disc, C+D Extrachorionic Matrix and G Extrachorionic Nipple-shaped Structure.

Nomenclature of the eggshell layers has thus clearly become confused, the innermost major structure (A+B+F) being referred to as Vitelline Membrane, Endochorion, or Exochorion, the outer structure (principally C, but some authors include D and/or G) as Endochorion, Exochorion, Spumaline, or Extrachorionic Matrix, and surrounding jelly layer D as Exochorion, Spumaline, or (with C) as Gelatinous Membrane. Nomenclature of apical structures is likewise confused, Pedicel and Apical Disc being used for F and Pedicel also for G. The revised nomenclature shown in Figure 1 may serve to correct these problems.

DISCUSSION

No familial characters separate eggs of Corduliidae from Libellulidae, and no subfamilial characters, except the hyperboloid micropylar projection and apical, recessed atrial openings of the Synthemistinae, separate the subfamilies examined. Variations in egg dimensions, egg development, colour, size of pedicel, size of micropylar projection, placement of atrial openings, chorion thickness, egg surface markings and gelatinous layers occur at generic and species level but are not correlated with higher classification. It follows that with the exception of well defined regional faunas, egg identification at below superfamily level is likely to be difficult and unreliable in Corduliidae and Libellulidae, and production of a general key to libelluloid eggs may not be possible.

Eggs are mostly ellipsoidal when laid, but in a majority of species the endochorion becomes more nearly spherical during development. Change in exochorionic shape appears limited to expansion of the gelatinous coating and passive distortion to accommodate the endochorion. These observations suggest, contra ANDO (1962), that the distinction between eggs which are ellipsoidal and eggs which are sub-spherical has no phylogenetic significance in this superfamily.

The endochorion, in all species examined, is smooth, is colourless or lightly coloured yellow to orange-brown when laid, and turns a deeper brown after a few hours or days. The exochorion is smooth or may carry follicle cell impressions, is colourless to light-grey when laid, and does not darken during development. Personal observation of oviposition in *Synthemis* regina suggests that the strongly developed follicle-cell patterned ridges on the surface of the exochorion are

probably associated with its habit of ovipositing by inserting the abdomen vertically into bottom mud in shallow water at the sides of the ponds in which it breeds.

In four of the species examined live, *D. melanopsis, H. australiae, H. tau,* and *P. jacksoniensis,* the outermost exochorionic layer expands after oviposition to form a gelatinous coating around the egg. Similar coatings have been noted in other libelluloids (CORBET, 1962; HINTON, 1981). The precursor layer may be present in other species but fails to expand or to become noticeably sticky, though some eggs readily accumulate a layer of fine debris which is not easily removed. Eggs of *H. australiae* and *H. tau* possess a second gelatinous investment in the form of thin strands forming basal attachments between eggs. These strands are present at oviposition and persist throughout development, but become obscured by expansion of the gelatinous layer around the egg. The strands can be stretched from less than 1 mm to over 50 mm in eggs up to 24 hours post-oviposition, and appear similar to strands previously described from *P. grayi* (WINSTANLEY, 1981) but are thinner and less robust. Eggs of *P. grayi* obtained for this study were embedded in dense jelly, but detailed strand structure was lost in preservation and could not be examined.

The endochorion and exochorion are closely apposed in some species but loosely connected in others. An intra-chorionic gap to 0.04 mm wide is visible in live eggs of several species, and wider separation occurs in preserved specimens. In some species, dissociation of layers during normal development may result in loss of initial alignment between the micropylar projection and pedicel, causing orientation of the embryo and endochorion to become haphazard with respect to the outer structures of the egg. In *H. australiae* and *D. melanopsis,* mechanical removal of the exochorion 6-10 days after oviposition has no noticeable effect on hatching success.

Atrial openings are presumed to be sites for sperm entry to the atrium and their position suggests a function in scooping sperm from the spermatheca during oviposition. The orientation of eggs in the oviduct, with micropylar projections facing backward and alternately left and right of centre, toward the spermatheca, supports this view. Existence of a two-step fertilization mechanism, with sperm mechanically scooped into the atrium during oviposition but only later penetrating the endochorion, would explain how exophytic dragonflies can sustain very high oviposition rates (a question raised by MILLER, 1987), and may also help explain the failure (as reported by DUNKLE, 1980) of past attempts at fertilization of dragonfly eggs *in vitro.*

ACKNOWLEDGEMENTS

I thank K.L. GARDNER for field assistance, K.A.J. WISE and J.A.L. WATSON for access to specimens, R. HEADY for technical assistance, and P.J. GULLAN for advice and comments on several drafts.

REFERENCES

ANDO, H., 1962. *The comparative embryology of Odonata with special reference to the relic dragonfly Epiophlebia superstes Selys.* Japn Soc. Promot. Sci., Tokyo.

ARMSTRONG, J.S., 1958. The breeding habitats of the Corduliidae (Odonata) in the Taupo district of New Zealand. *Trans. R. Soc. N.Z.* 85(2): 275-282.

BEAMS, H. & KESSEL, R., 1969. Synthesis and deposition of oocyte envelopes (vitelline membrane, chorion) and uptake of yolk in the dragonfly (Odonata: Aeshnidae). *J. Cell Sci.* 4: 241-264.

CORBET, P.S., 1962. *A biology of dragonflies.* Facsimile reprint, Classey, Farringdon [1983].

DUNKLE, S.W., 1980. *Second larval instars of Florida Anisoptera (Odonata).* Ph. D. Thesis. Univ. Florida, Gainesville.

GONZALEZ SORIANO, E., 1987. Dythemis cannacrioides Calvert, a libellulid with unusual ovipositing behaviour (Anisoptera). *Odonatologica* 16(2): 175-181.

HINTON, H.E., 1981. *Biology of insect eggs.* Oxford, Pergamon Press.

IVEY, R.K., J.C. BAILEY, B.P. STARK & D.L. LENTZ, 1988. A preliminary report of egg chorion features in dragonflies (Anisoptera). *Odonatologica* 17(4): 393-399.

KAWASAKI, H., H. SATO & M. SUZUKI, 1974. Structural proteins in the egg envelopes of dragonflies Sympetrum infuscatum and S. frequens. *Insect Biochem.* 4: 99-111.

McCRAE, A.W.R. & P.S. CORBET, 1982. Oviposition behaviour of Tetrathemis polleni (Selys): a possible adaptation to life in turbid pools (Anisoptera: Libellulidae). *Odonatologica* 11(1): 23-31.

MILLER, P.L., 1987. Oviposition behaviour and eggshell structure in some libellulid dragonflies, with particular reference to Brachythemis lacustris (Kirby) and Orthetrum coerulescens (Fabricius) (Anisoptera). *Odonatologica* 16(4): 361-374.

MILLER, P.L. & A.K. MILLER, 1985. Rates of oviposition and some other aspects of reproductive behaviour in Tholymis tillarga (Fabricius) in Kenya (Anisoptera: Libellulidae). *Odonatologica* 14(4): 287-299.

ROWE, R., 1987. *The Dragonflies of New Zealand,* Auckland Univ. Press, Auckland.

TILLYARD, R.J., 1911. On the genus Cordulephya. *Proc. Linn. Soc. NSW.* 36: 388-422.

TILLYARD, R.J., 1917. *The Biology of Dragonflies.* Cambridge Univ. Press, Cambridge.

WARINGER, J., 1983. A study on embryonic development and larval growth of Sympetrum danae (Sulzer) at two artificial ponds in lower Austria (Anisoptera: Libellulidae). *Odonatologica* 12(4): 331-343.

WINSTANLEY, W.J., 1981. A unique egg strand in Procordulia grayi (Selys) (Anisoptera: Corduliidae). *Odonatologica* 10(1): 57-63.